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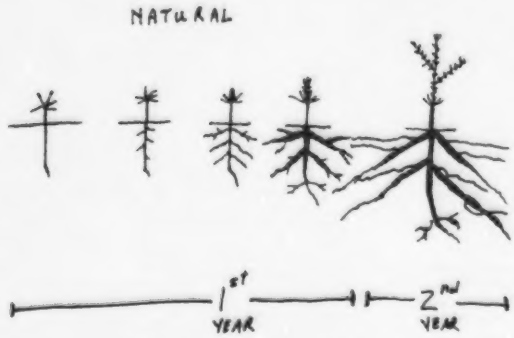
P. Salonius, K. Beaton, and B. Roze



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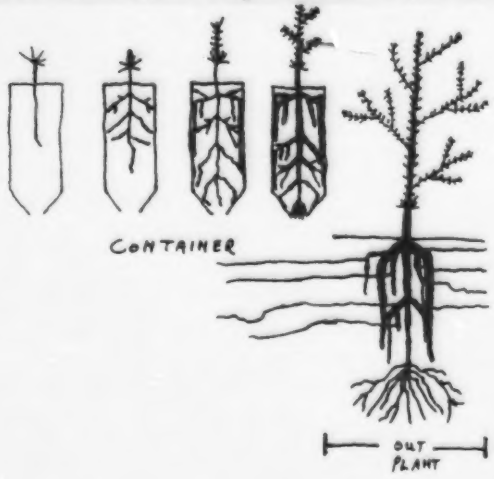

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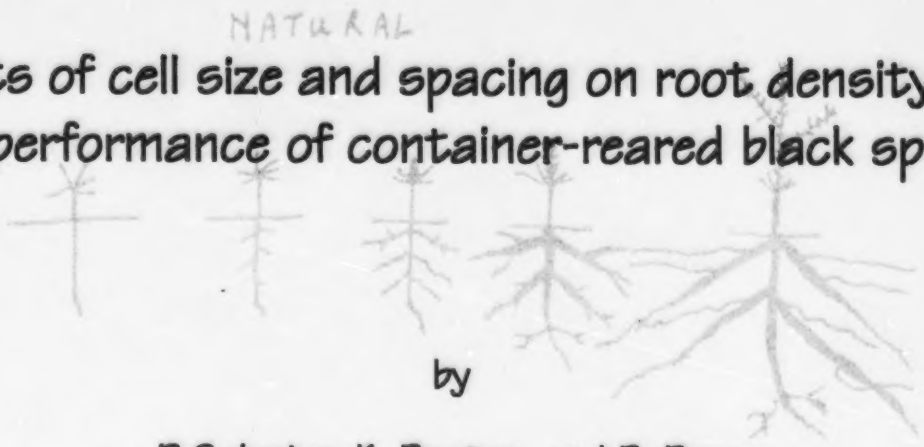

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by

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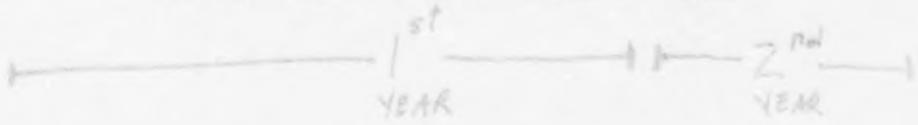

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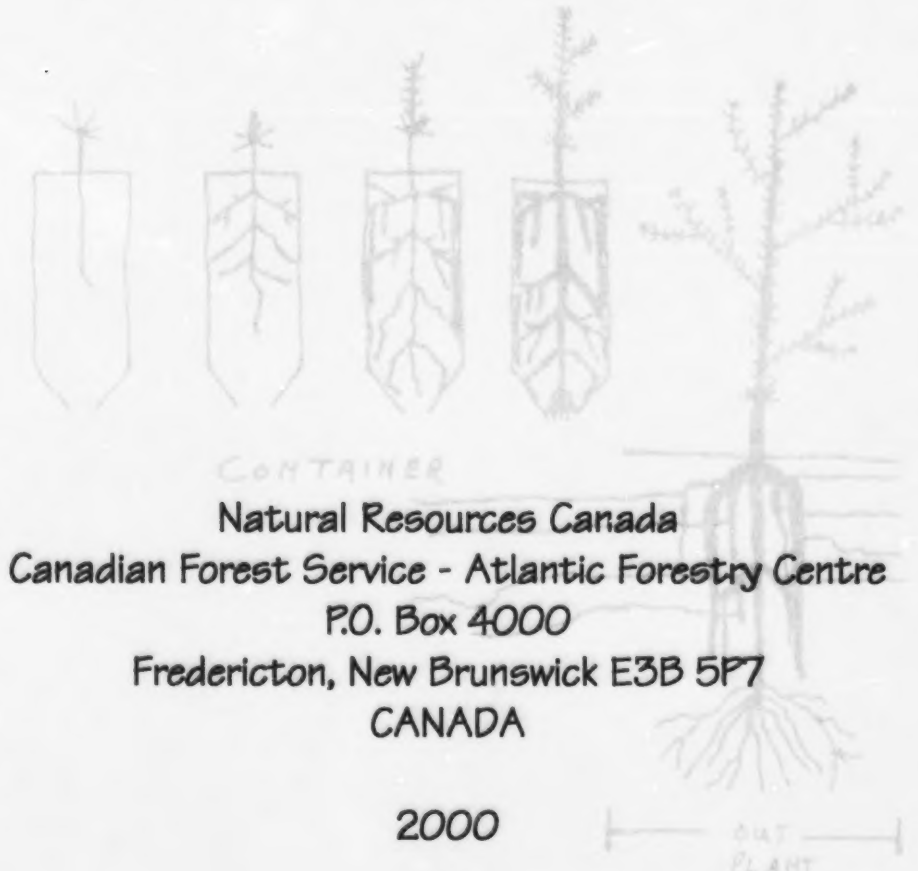

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Abstract

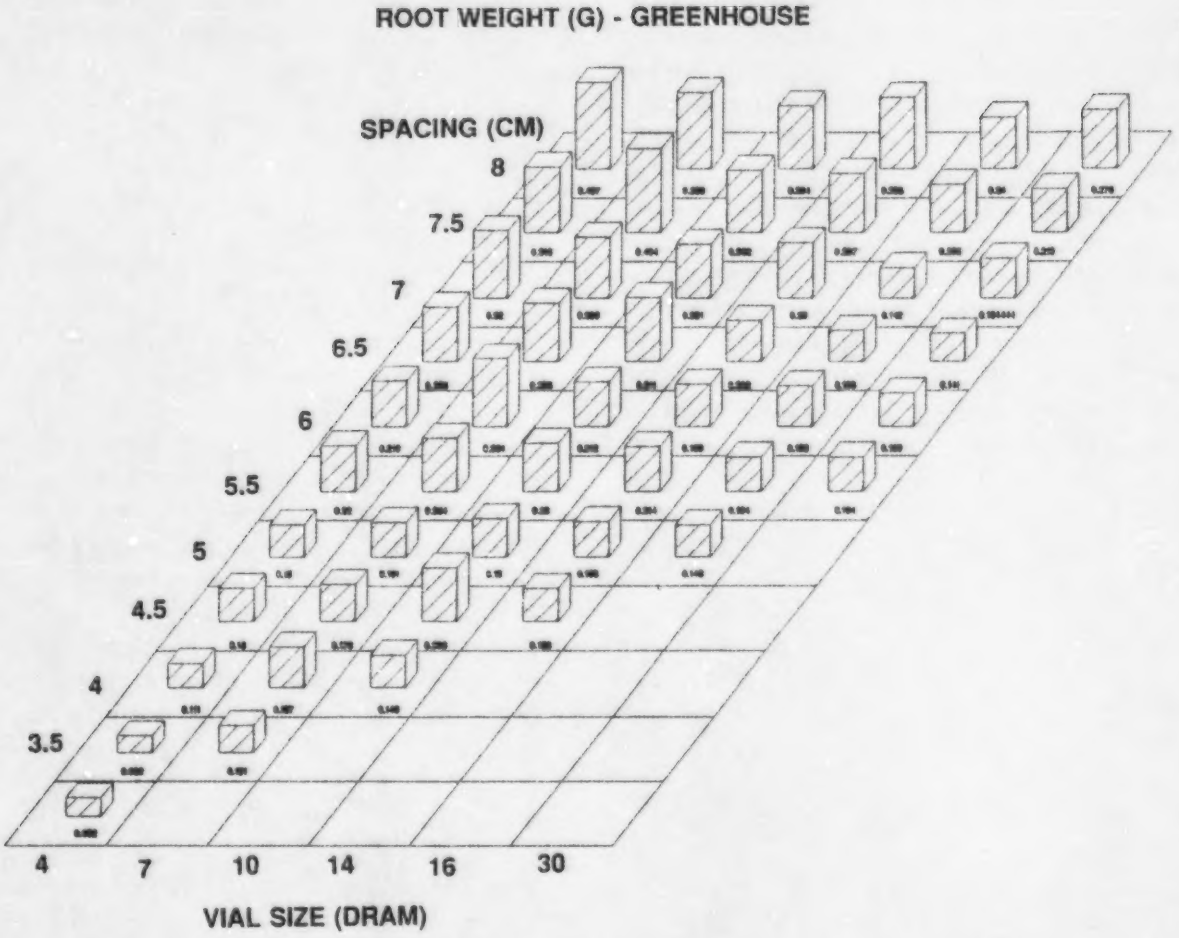
This study examined the effects of nursery rearing in an array of 51 individual fabricated frames that supported a range of six growing cell sizes at 11 plant spacings in all possible combinations. A continuum of seedling crowding was achieved by placing the same sized cells closer together or by increasing cell size at the same spacing such that soil surface represented 6.2 to 60.4% of horizontal growing space. As seedlings were increasingly crowded during rearing, photosynthate partitioning favored aerial plant parts, shoot:root ratios increased, and soil plugs were less firmly held together by the roots. Decreased crowding produced lower shoot:root ratios and very firm, "root-bound" plugs with high root densities. Soft, undergrown plugs grew roots more actively in field outplantings than did hard, overgrown plugs. These results are discussed in the context of production practices that extend nursery growing to produce large seedlings with high root plug integrity.

Key words: Soil plug size, plant spacing, nursery growth and morphology, root density, root regeneration, field growth performance.

Abrégé

La présente étude a pour objet d'examiner les effets de la culture en pépinière de semis organisés en un jeu ordonné d'échantillons comptant 51 cadres-supports ouvrés supportant une plage de six tailles de cellules croissantes, selon 11 espacements de plantes, dans toutes les combinaisons possibles. On a réalisé une séquence d'entassement des semis, en rapprochant les cellules de même taille les unes des autres, ou en augmentant la taille des cellules situées au même emplacement, de sorte que la surface du sol représente de 6,2 à 60,4 % de la surface de croissance horizontale. Étant donné que les semis ont été entassés graduellement au cours de la culture, le partage du photosynthétat a favorisé les parties aériennes des plantes; les rapports pousses:racines se sont accrus et les mottes étaient moins fermement retenues ensemble par les racines. La réduction de l'entassement a produit des ratios pousses:racines moins élevés et des mottes à racines « feutrées » très fermes, ayant des densités radiculaires élevées. Les mottes molles et petites transplantées à l'extérieur ont développé des racines plus activement que les mottes dures et grosses. Ces résultats sont analysés dans le contexte des pratiques de production qui prolongent la période de croissance en pépinière afin de produire de gros semis à pelotes radiculaires de haute intégrité.

Mots clés : taille des mottes, espacement de plantes, croissance en pépinière et morphologie, densité radiculaire, régénération des racines, rendement en matière de croissance en plein champ.


ROOT WEIGHT (G) - GREENHOUSE
SPACING (CM)
8
7.5
7
6.5
6
5.5
5
4.5
4
3.5
4
7
10
14
16
30
VIAL SIZE (DRAM)

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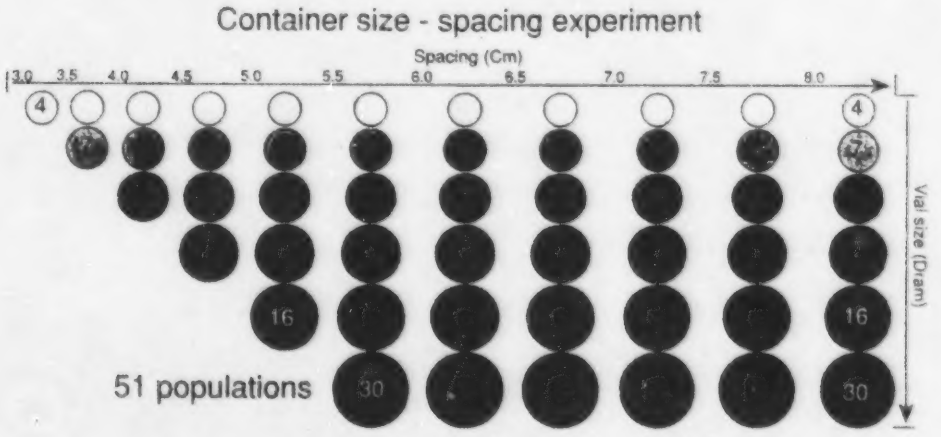
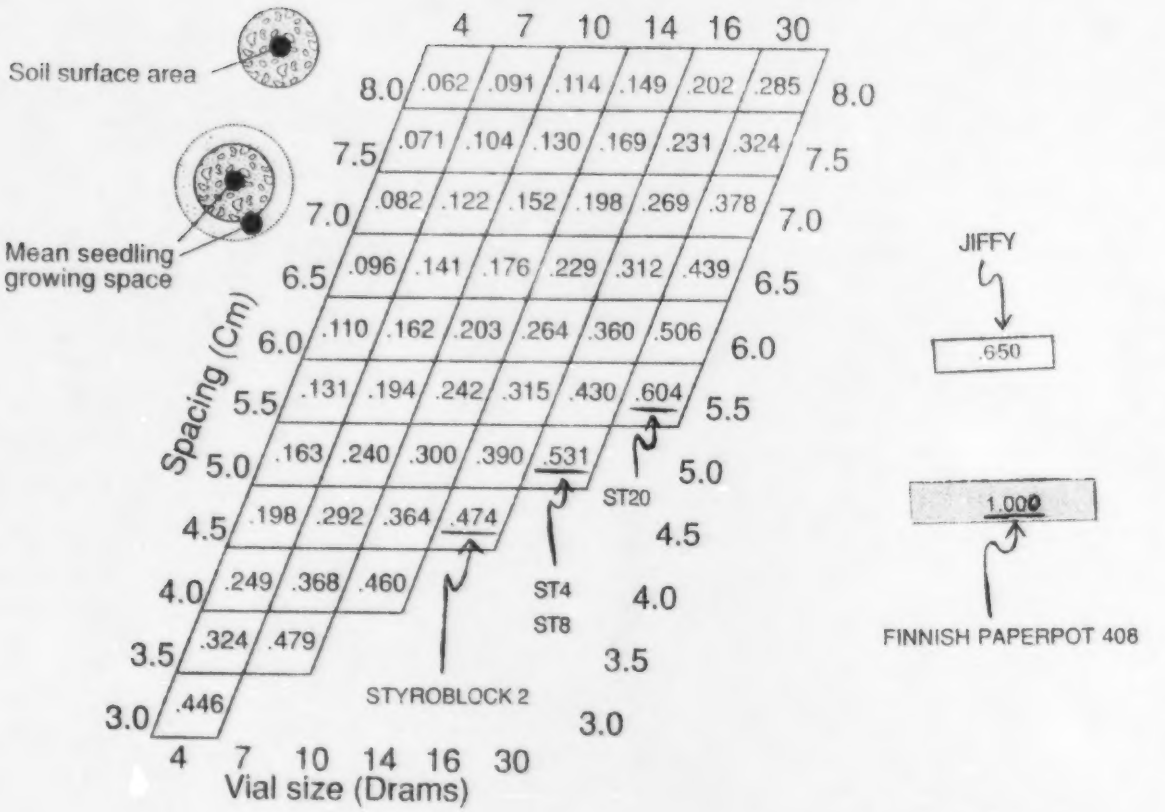




$$\text{Soil-space Ratio} = \frac{\text{soil surface area (Cm}^2\text{)}}{\text{Mean seedling growing space (Cm}^2\text{)}}$$

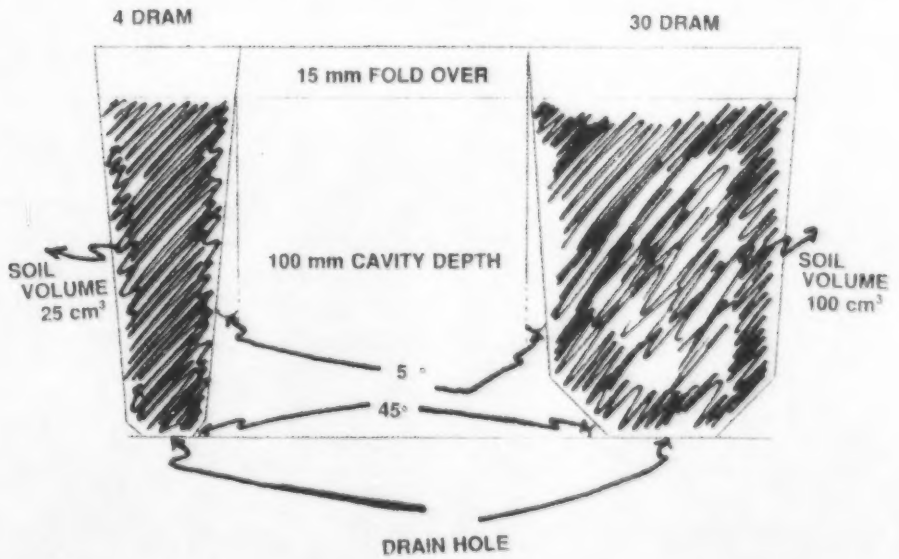
Introduction

There has been an increasing trend toward larger container-reared forest nursery stock in recent years (Brazier 1991; Balisky *et al.* 1995). Larger stock is seen as being necessary to compete with non-crop vegetation, previously controlled by intense mechanical site preparation and by chemical herbicide; these controls are now less prevalent because of legislative controls (Jobidon *et al.*, 1998).

The influence of rearing density on the size and outplanted growth performance of bare-root nursery seedlings has been reported by Van den Driessche (1982, 1984) and Caufield *et al.* (1987).

Endean and Carlson (1975) and Carlson and Endean (1976) conducted experiments into the effects of different container cell volumes and lengths upon the size attained by seedlings in the nursery at set plant spacings, while Timmis and Tanaka (1976) studied the growth of seedlings in cells of a set volume at various plant spacings. Barnett and Brissette (1986) and Simpson (1991) found that the principal factor causing growth differences in container systems was cell density rather than cell shape or volume. Calculations based on the results of Simpson (1991) show a marked decrease in seedling root density in container rearing soil as same-sized cells were increasingly crowded in the nursery. Studies of the effects of growing density and other container attributes on seedling growth in forest nurseries have been confounded by variations in cell diameter, length, and volume, which are imposed by the commercially manufactured containers that have been used in the experiments (Sutherland and Day 1988; Simpson 1991). Boudoux (1972), Endean and Carlson (1975), Timmis and Tanaka (1976), and Carlson and Endean (1976) fabricated growing cells for container-rearing experiments so as to avoid the disparate types of commercially manufactured container systems.

The original object of this study was to assess the relative merits of either increasing seedling rearing cell diameter or increasing between-cell growing space to produce larger forest seedling stock for plantation establishment. The results of the two similar experiments presented here describe the effects of various combinations of cell diameters and spacings on the greenhouse growth of conifer seedlings and the performance of these seedlings after the stressful transition from greenhouse to field growth.



Material and Methods

Experimental Container Units

Individual plant growing cells were constructed using a gas-impermeable plastic film (Saranex®, Dow Canada Inc.) that could be heat sealed. All cells were 100 mm long and had tapered side walls 5° from vertical. The area of the drainage hole at the cell base was 20% of the area of the soil surface. The steeper taper from the edge of the drainage hole to the junction with the side wall was 45° from horizontal. The fabricated cells had an extra 15 mm length which was folded over the top edge of a pharmaceutical vial from which the closed bottom had been cut off (2 cm of the top of the vial remained). This folded-over part of the plastic film was held tightly in place with the "snap on" vial cap whose center had been cut out except for a residual 2-mm rim. Holes were drilled through 1-cm thick exterior grade plywood tops of individual support frames such that the cut-off vials would slide through while the extra diameter of the "snap on" cap prevented the entire soil-containing cell from falling through the hole. The 51 individual support frames (each with specific cell size and spacing) had enough holes to accommodate the 40 hanging cells required for the study. The support frames had sufficient extra cells so that the two outside edge rows of each unit served as unused buffers with the neighboring frames on the greenhouse bench, which harbored populations of seedlings with other combinations of cell diameter and plant spacing. The 150-mm solid plywood side walls supporting the plywood tops allowed the hanging soil-filled cells uninterrupted access to air circulating through the metal mesh bench surface that was 1 m above the greenhouse floor. The same 51 plywood support frames with hanging growth cells were used for both greenhouse rearings (1990 and 1992) reported here.

The plant growth cells were arranged at 11 spacings from 3-8 cm apart (center to center) in an equidistant (isosceles) pattern. Inside diameters of the vials holding the plastic cells (and thus the diameter of the filled soil surface) were 21.0, 25.5, 28.5, 32.5, 38.0 and 45.0 mm, with soil volumes of 25, 35, 45, 55,70 and 100 mL respectively. The growing density of the seedlings ranged from 179 to 1290 seedlings/m^2 (Table 1). Arrangements with the larger cell sizes at the five closest plant spacings were not physically possible (Table 1). A shortage of greenhouse bench space precluded randomization of the various treatments because plywood support frames with the widest cell spacing were many times larger (0.56 m^2) than those with the narrowest cell spacing (0.11 m^2). Cultural conditions were homogeneous throughout the greenhouse; circulation fans ran constantly and nozzles on the travelling irrigation boom were maintained free of obstructions.

A descriptive parameter was developed to describe the degree of crowding produced by the various combinations of cell diameter and plant spacing; this parameter is the ratio of the soil surface area inside the plastic cell to the mean areal horizontal growing space for each seedling. The mean areal horizontal growing space is larger than the soil surface area because of the space between the cells. This soil:space ratio increases as cells of the same size are placed closer together and it also increases as cells at the same spacing increase in size (Table 1). The soil:space ratio may be thought of as an index of crowding. A soil:space ratio of 1.0 would describe container systems, such as paperpots, that have no space between individual cells. The soil surface area of the cells in the 51 individual plywood support frames occupied from 6.2 to 60.4% of the horizontal areal growing space (Table 1).

Table 1. Soil:space ratio and growing density of experimental container units

Plant Spacing (cm)	Growth Cell Diameter (mm)						Density (seedlings/m^2)
	21	25.5	28.5	32.5	38	45	
	Soil : space ratio						
8	0.062	0.091	0.114	0.149	0.202	0.285	179
7.5	0.071	0.104	0.13	0.169	0.231	0.324	204
7	0.082	0.122	0.152	0.198	0.269	0.378	238
6.5	0.096	0.141	0.176	0.229	0.312	0.439	276
6	0.11	0.162	0.203	0.264	0.36	0.506	318
5.5	0.131	0.194	0.242	0.315	0.43	0.604	380
5	0.163	0.24	0.3	0.39	0.531	-	470
4.5	0.198	0.292	0.364	0.474	-	-	571
4	0.249	0.368	0.46	-	-	-	721
3.5	0.324	0.479	-	-	-	-	937
3	0.446	-	-	-	-	-	1290

- Not possible, due to cell overlap

Nursery Culture

Two complete rearings were carried out, one as a winter crop in 1990 and the other as a summer crop in 1992. Cells were filled with a peat:vermiculite (2:1) "soil" mix, and this "soil" was then thoroughly wetted by overbench travelling boom irrigation such that the wet soil surface was approximately 1 cm below the lip of the cell; this depression accommodated seed and a 5-mm lime grit application to cover the seed. Black spruce (*Picea mariana* [Mill.] B.S.P) was manually sown with four seeds per cell to ensure full occupancy in early February for the 1990 winter greenhouse crop and in mid-May for the 1992 summer greenhouse crop. The greenhouse was maintained at 25°C for the 3-week germination period and supplemental light was provided for 2 hours during the night to avoid bud set. Fertilizer (forestry starter) solutions, containing 5 ppm nitrogen, were applied every 2 hours as a mist during the 3-week germination period. The greenhouse was maintained at a day temperature of 22°C and a night temperature of 18°C during the growing period. After the germination was complete, irrigation to soil saturation and run-through was carried out at least three times weekly to ensure that water deficits did not develop and that seedlings in the various cell sizes had access to the same fertilizer concentrations at all times during the growing period. Nitrogen in fertilizer solutions (forestry grower), used at each irrigation,

began at 25 ppm and increased in 25-ppm steps every 2 or 3 weeks so that the plants were receiving 125 ppm during week 15 after seeding. At the end of the period of exponential growth, supplemental night lighting was withdrawn to facilitate hardening of succulent tissue before field planting. Leaching of residual fertilizer from the soil was carried out with heavy applications of water for 24 hours and then regular irrigation was supplied for 2 weeks with water only. After 2 weeks without fertilizer, the 1990 winter greenhouse was irrigated with forestry finisher fertilizer solution at 35 ppm nitrogen during June; these seedlings were field planted at 21 weeks from seeding in early July. The 1992 summer greenhouse crop received finisher solution throughout the autumn after the withdrawal of night lighting, leaching and water irrigation, with the greenhouse maintained near outdoor temperatures after terminal bud formation was detected (Carlson 1983); these seedlings were stored frozen in sealed boxes and field planted in May of 1993.

Destructive Characterization before Outplanting

Preplanting seedling characteristics were obtained from a subsample of 20 seedlings from the interior rows of each of the 51 populations. Roots were washed free of soil, and seedling height, root collar diameter, and oven-dry shoot and root weights were recorded.

Field Design and Outplanting

During the first week of July 1990, the 20 remaining black spruce seedlings from the interior rows of the winter greenhouse crops of each population were removed from the support frames. Seedlings were extracted from the plastic growth cells at the moment of planting. The planting design, in a former bare-root nursery field, consisted of five-tree rows of specified seedling populations running north-south in tilled strips, and running east-west in four blocks. Population numbers within the blocks were completely randomized. The five-tree rows were 38 cm apart and the seedlings were 25 cm apart within the rows. The same protocol was followed for the 1992 summer greenhouse crop after the seedlings were removed from frozen storage and thawed in May of 1993.

Destructive Characterization of Field-Grown Seedlings

At the end of one growing season in the field, during October 1990, all 20 seedlings from the 1990 winter greenhouse crop were excavated. Soil was gently shaken off the roots which were then washed free of field and residual greenhouse soils. Seedling height, root collar diameter, and oven-dry shoot and root weights were determined. During October 1993, the outplanted 1992 summer greenhouse crop was excavated and submitted to the same destructive characterization upon the completion of one field growing season.

Analysis of Nursery Growth and Field Performance

Mean seedling characteristics at the end of nursery rearing were plotted as scattergrams against the soil:space ratios of the fabricated container patterns in which they were reared. The mean population percent shoot and root weight increases, after one field growth season, were plotted as scattergrams against root densities in soil plugs at outplanting. Graphical treatments to apply cubic polynomial curves to scattergrams were done using Microsoft Excel Version 5.0 (1994).

Results

Seedling Characteristics after Nursery Rearing

Seedling height at the end of the nursery rearing period increased as soil:space ratio increased for both the 1990 winter-reared crop (Fig.1) and the 1992 summer-reared crop (Fig. 2). Shoot growth was progressively emphasized over root growth (higher shoot:root ratios) as soil:space ratio increased for both crops (Figs. 3 and 4). Shoot:root ratios were higher for the 1990 winter crop (Fig. 3), which continued height growth as a result of long day length during the hardening off process. Root density (mg root/cm^3 soil) decreased as soil-space ratio increased for both crops (Figs. 5 and 6). Root density was considerably higher for the summer-reared 1992 crop (Fig. 6) because root growth continued for two months after the cessation of height growth and the formation of terminal buds during the short days of autumn. Lighter-rooted soil plugs, especially those from high soil:space ratios in the 1990 winter crop, were more fragile and had to be handled very carefully to avoid soil loss as they were extracted from the plastic cells at the time of planting. There was a general trend for seedlings to become more slender and spindly (increasing height:root collar diameter ratio) as crowding expressed by soil:space ratio increased. An increase in seedling side branching was apparent as crowding and competition for light became less intense, but this was not quantified.

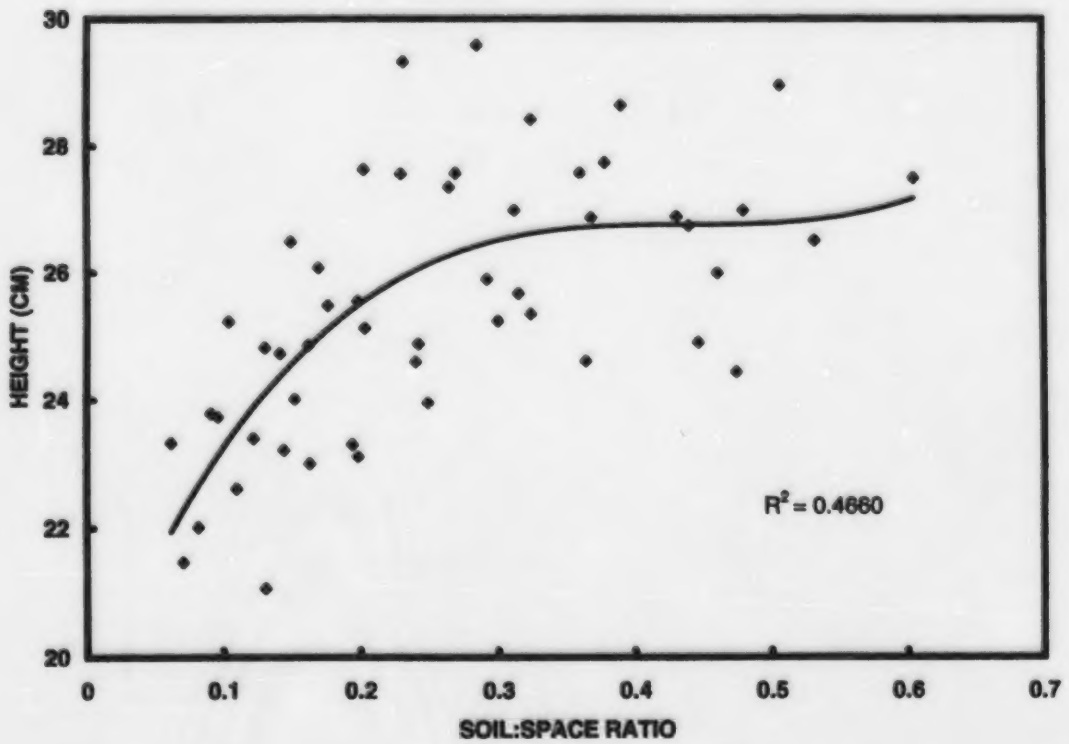


Figure 1 Relationship of seedling height to soil:space ratio at the end of 1990 winter greenhouse rearing (points are 20-seedling means)

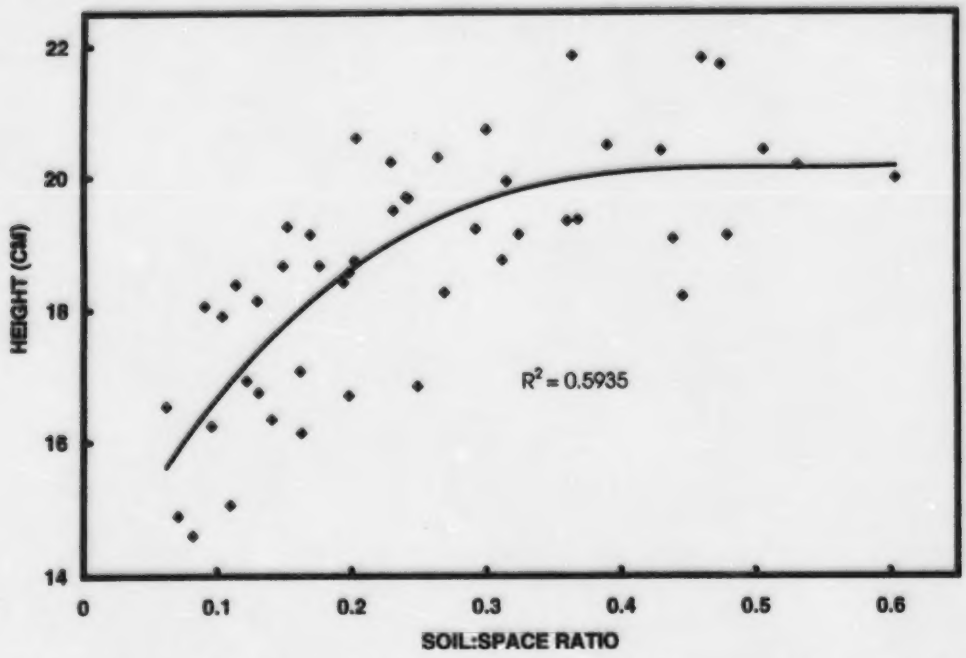


Figure 2 Relationship of seedling height to soil:space ratio at the end of 1992 summer greenhouse rearing (points are 20-seedling means)

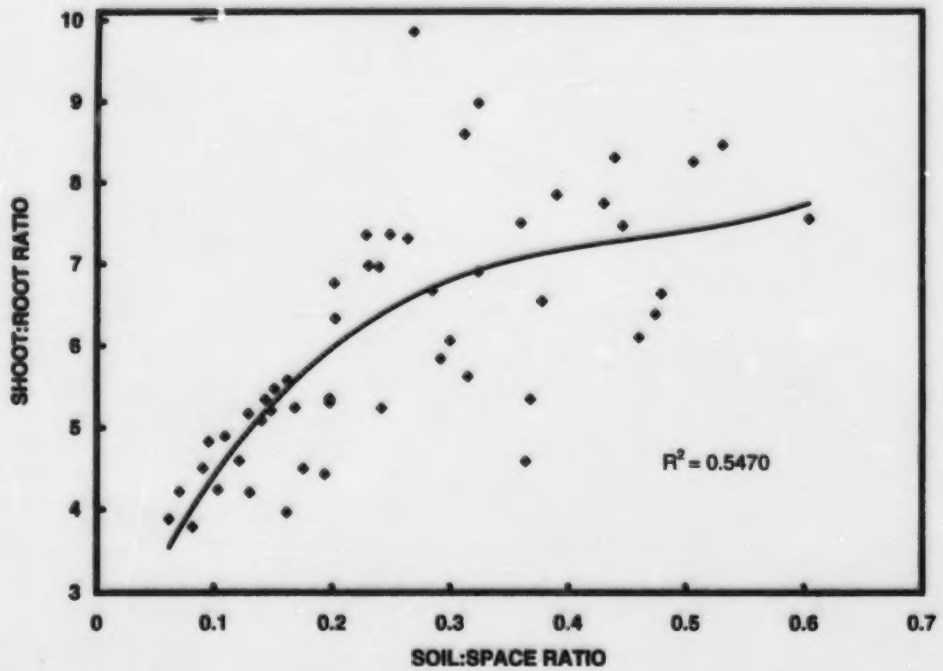


Figure 3 Relationship of population shoot:root ratio to soil:space ratio at the end of 1990 winter greenhouse rearing (each point represents one of 51 populations)

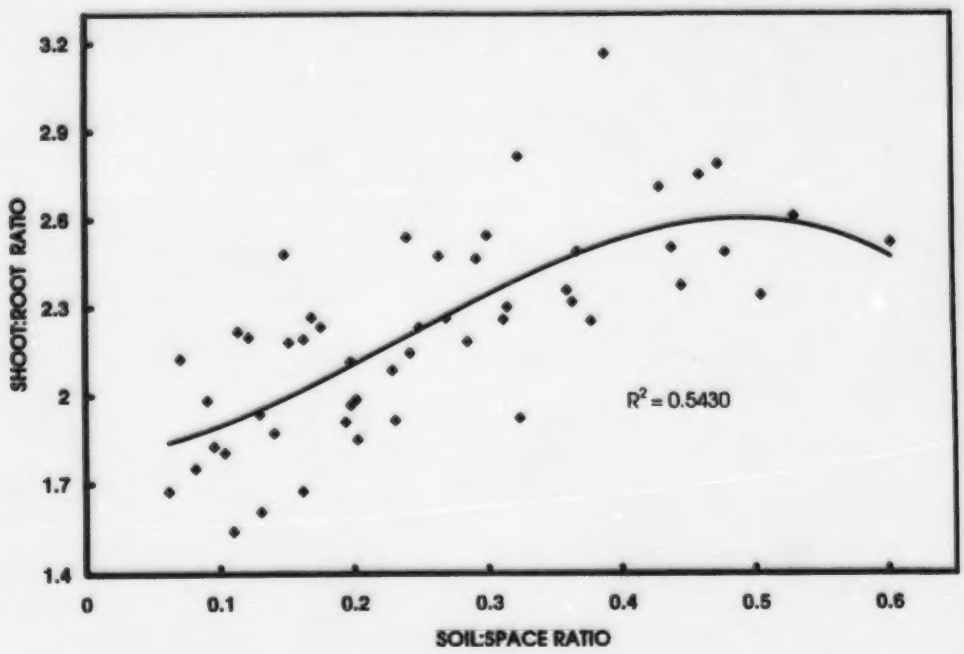


Figure 4 Relationship of population shoot:root ratio to soil:space ratio at the end of 1992 summer greenhouse rearing (each point represents one of 51 populations)

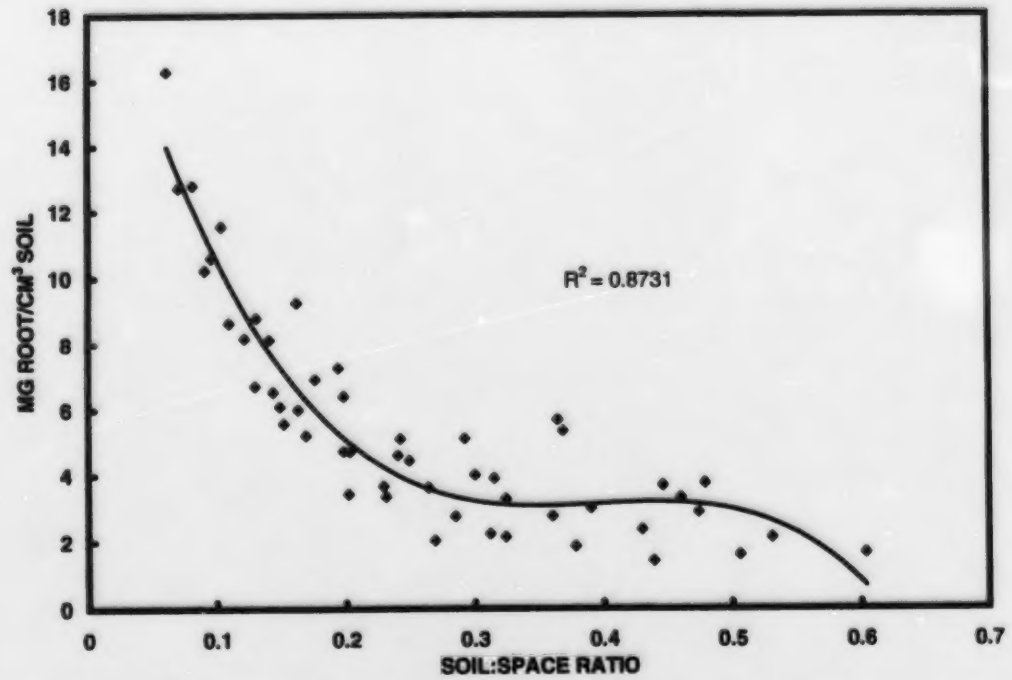


Figure 5 Relationship of root density (mg root/cm³ soil) to soil:space ratio at the end of 1990 winter greenhouse rearing (points are 20-seedling means)

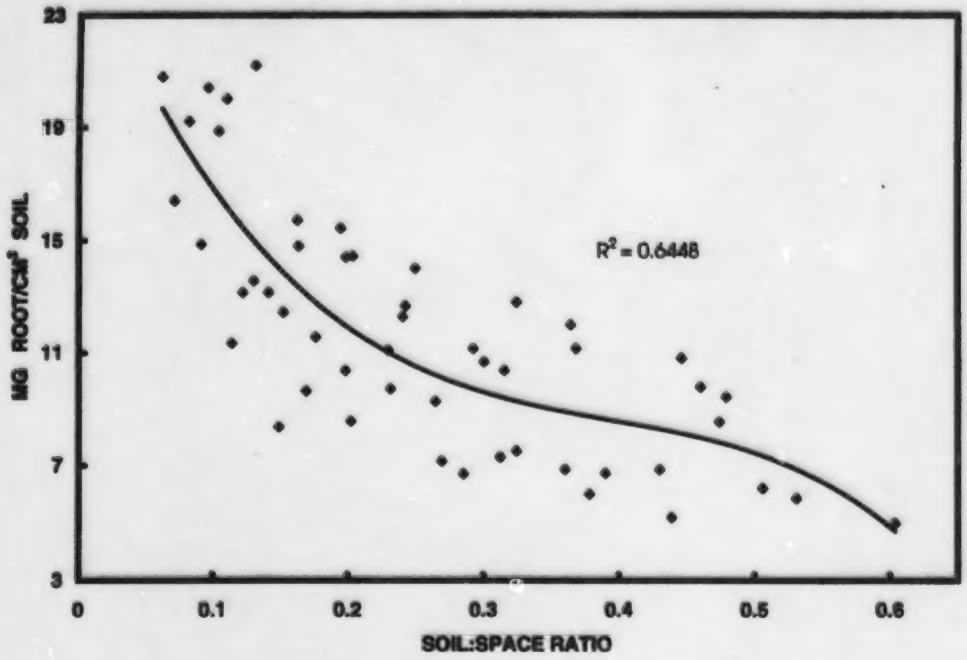


Figure 6 Relationship of root density (mg root/cm³ soil) to soil:space ratio at the end of 1992 summer greenhouse rearing (points are 20-seedling means)

Seedling Field Performance

As a result of high regression coefficients between nursery root density and the crowding measure (soil:space ratio) for the individual growing cell arrangements (Figs. 5 and 6), we plotted growth performance in the first field season against both root density and soil:space ratio. As seedling growth during the first field season after outplanting was consistently better correlated with nursery root density than with soil:space ratio, only the relationships between nursery root density and field growth are presented here. Shoot growth during the first field outplant season decreased as nursery root density increased in response to decreased crowding for both the 1990 winter greenhouse (Fig. 7) and 1992 summer greenhouse (Fig. 8) crops. Root growth after outplanting also decreased as less intense crowding produced increased greenhouse root density (Figs. 9 and 10). The most active field growth of roots was produced by the most lightly rooted plugs, which had been produced in growth cell arrangements with the highest soil:space ratios.

Summary of Crowding Effects

This study has shown that the decrease in seedling growing space resulting from crowding, which is described by increased soil:space ratios, produced increases in height, shoot:root ratios, and height:root collar diameter ratios (data not presented). Crowding also produced thinner crowns, less side branching (data not presented), and less firm soil plugs with lower root density. Roots from crowded cell arrangements, that were more juvenile and less suberized, grew more actively in the outplanting field soil during what might be considered to be a season-long root regeneration test.

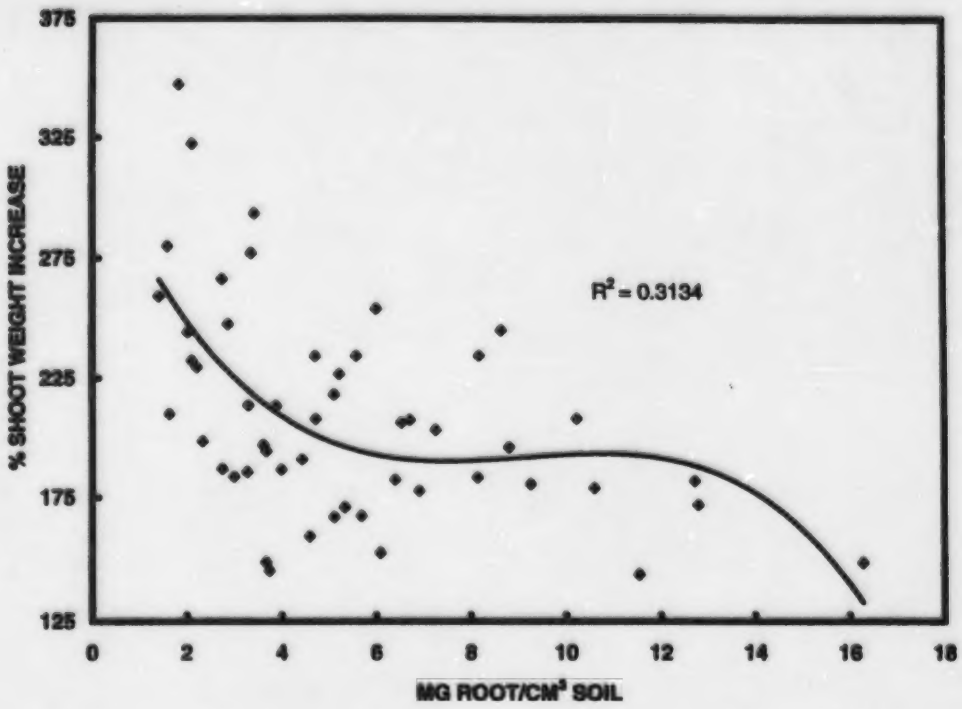


Figure 7 Relationship of population shoot weight increase, in the first field outplant season, to population root density at the end of greenhouse rearing of the 1990 winter crop (each point represents one of 51 populations)

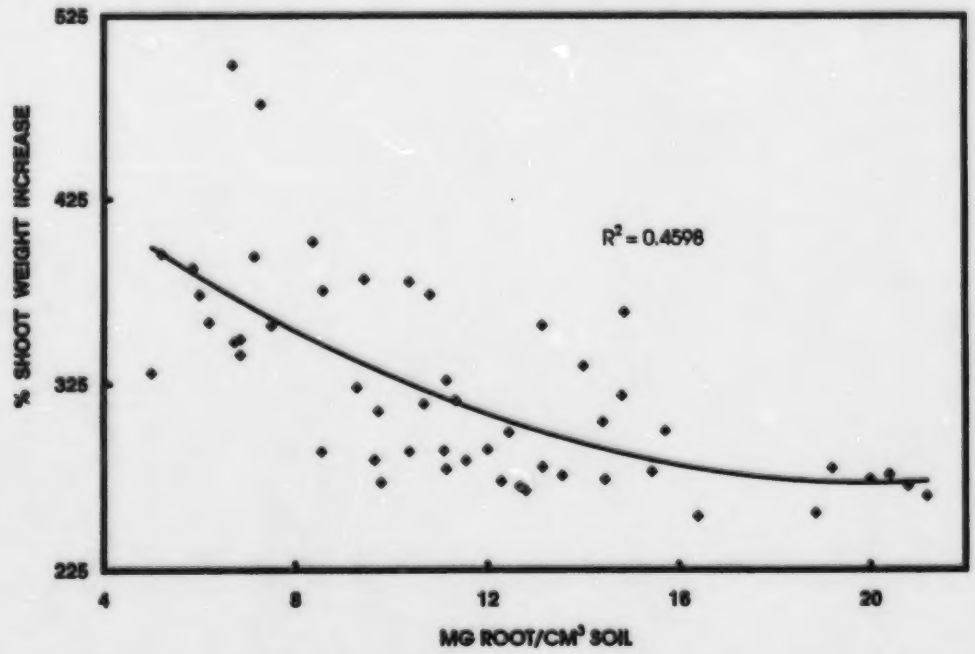


Figure 8 Relationship of population shoot weight increase, in the first field outplant season, to population root density at the end of greenhouse rearing of the 1992 summer crop (each point represents one of 51 populations)

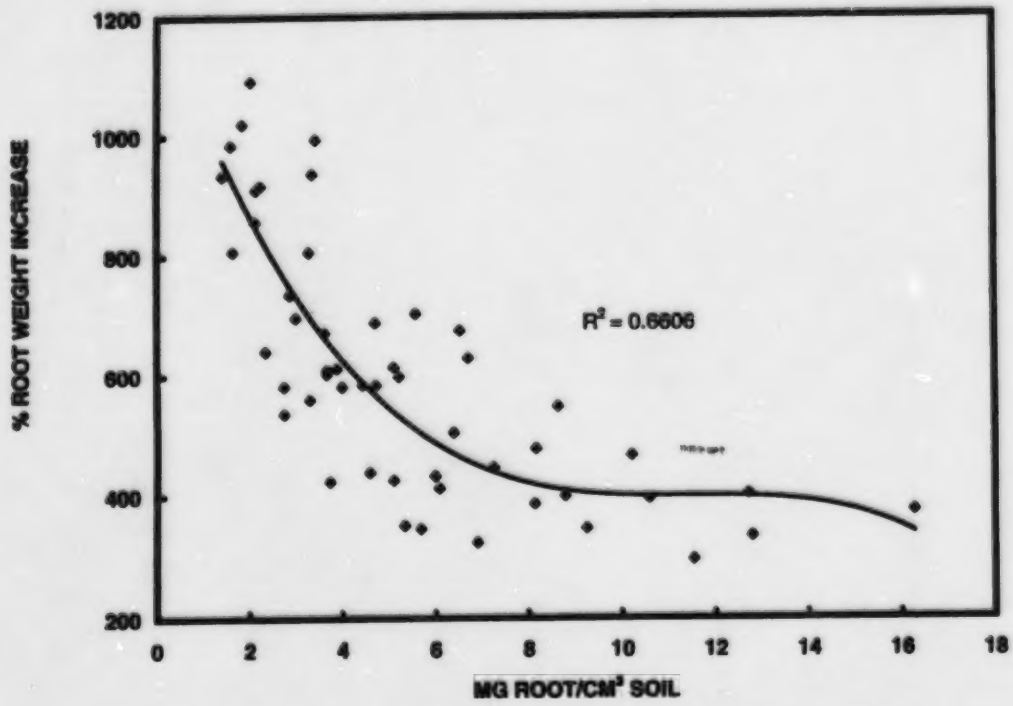


Figure 9 Relationship of population root weight increase in the first field outplant season to population root density at the end of greenhouse rearing of the 1990 winter crop (each point represents one of 51 populations)

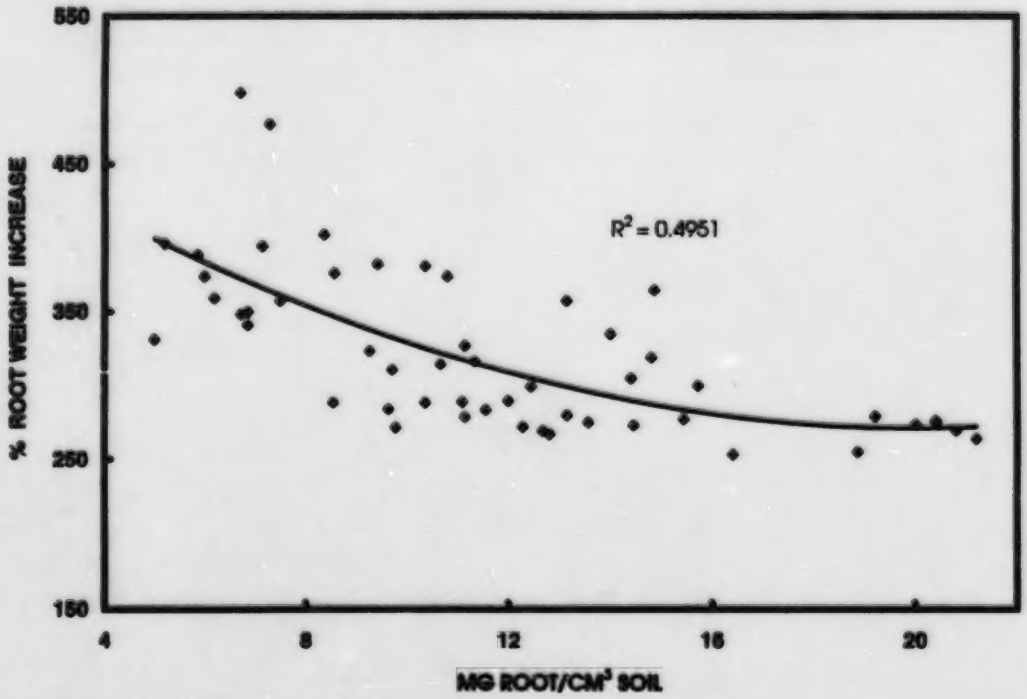


Figure 10 Relationship of population root weight increase in the first field outplant season to population root density at the end of greenhouse rearing of the 1992 summer crop (each point represents one of 51 populations)

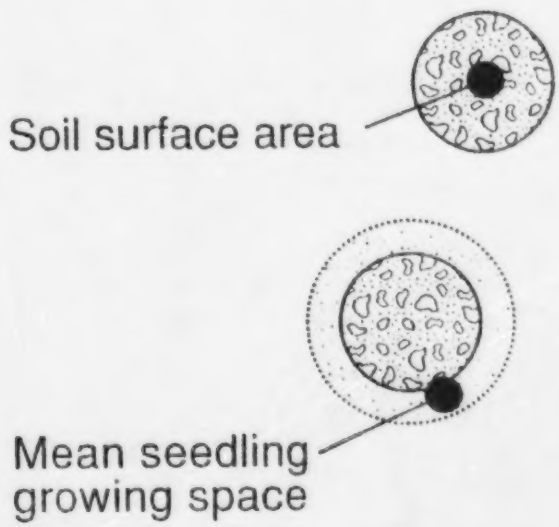
Discussion

The similarity in the results for the winter and summer black spruce crops serves to increase confidence in the generality of the response of container-grown seedlings to crowding during nursery rearing. It is expected that the results of this study with black spruce seedlings, reared in fabricated frames with various cell arrangements, will apply in principle to other species. Black spruce displays a high level of allocation plasticity in relation to light availability. Shading of conifer seedlings of other species has been found to cause shifts towards height growth and away from branch and root growth (Mitchell and Arnott 1995); such shifts in shoot:root ratios are indicative of changes in carbon allocation. Timmis and Tanaka (1976) and Simpson (1991) found that high-density rearing in container systems produced tall, thin conifer seedlings while low-density rearing produced short, stocky seedlings. Our study with black spruce supports these general observations. These observations are similar to those made in studies of bare-root nursery rearing density (Van den Driessche 1982, 1984; Caufield *et al.* 1987). Timmis and Tanaka (1976) referred to the parasitic nature of lower crown foliage that is deprived of light by mutual competition between seedlings grown at high densities. These needles do not get adequate light to support their metabolic requirements, so they draw photosynthetic assimilates from foliage higher in the crown where competition for light is not so intense. The tendency for seedlings to compensate for light limitation by allocating a larger proportion of total plant photosynthate to shoot growth, at the expense of root growth (Drew 1983), explains why root plugs of crowded seedlings were very fragile.

Operationally raised conifer seedlings in walled containers are usually shipped to the field with root densities greater than 4 mg/cm^3. Such firm soil plugs do not require careful handling to avoid serious disintegration after removal from growth cells. Endean and Carlson (1975) showed that as root density increased above 0.45 mg/cm^3 nursery growth rates of seedlings diminished. The root density levels in this study were consistently above 1 mg/cm^3, and they ranged as high as 16 mg/cm^3 as soil:space ratio or crowding decreased to produce increasingly "root-bound" seedlings. Simpson (1991) produced root densities as high as 60 mg/cm^3 at low container cell densities; he suggested that larger seedlings had greater field growth, but mean relative growth rates of seedlings were not affected by nursery growing density. Similar conclusions have been drawn concerning the original size advantage for bare-rooted seedlings and the absence of relative growth rate differences as influenced by rearing density (Van den Driessche 1982, 1984). This is in contrast to the results of the present study which suggest that growth rates (especially root growth rates) of field-planted seedlings decrease as nursery root density increases towards a "root-bound" condition in response to diminished rearing density or crowding. Crowding leads plants to devote a disproportionate amount of photosynthate to shoots, resulting in less mature roots whose more active field growth rates allow them to access increasing soil volumes adjacent to the planted plug. The poorest root regeneration in this study was seen for plants grown in the least crowded cell arrangements with the lowest soil:space ratios. When these plants with large, well-branched tops at wide spacings were influenced to moderate shoot growth during the hardening off process before outplanting, root weight increased tremendously. When the decrease in foliar tissue, due to increasingly dense rearing (Simpson 1991), is coupled with the observation that current photosynthate is the primary carbon source for new root growth (Philipson 1987; Van den Driessche 1987), the superior root growth of seedlings from crowded nursery conditions is surprising. This superior growth appears to result from a difference in the juvenility of the roots of crowded seedlings compared to the more suberized mature roots of open-grown seedlings. The benefit of juvenile roots appears to outweigh any advantage produced by increased photosynthetic tissue resulting from decreased crowding. Nursery-reared container seedlings are often submitted to extended residence in the growing cell to produce larger planting stock that

is supposed to be better able to compete with non-crop vegetation after outplanting. Extended residence in growing cells is also designed to increase root density in the soil plug so as to prevent disintegration during handling, transport, and outplanting.

Barnett and Brissette (1986) and Balisky *et al.* (1995) suggested that the development of deformed root systems increases rapidly with the length of time seedlings are grown in containers. Increased root deformation occurs when seedlings, grown at wide spacings with large foliage mass, are culturally influenced with low nitrogen and short day-length to slow shoot growth during the hardening off period. Uncrowded seedlings, with access to high light levels over the entire crown, directed large amounts of photosynthate to the roots during hardening. This disproportionate root growth would normally (for seedlings reared at higher densities) occur when high light levels are experienced in the field as a result of the wide plant separations produced by outplant spacing arrangements. Very vigorous root growth inside the less crowded container cells produced seedlings with high densities of suberized roots that were relatively unresponsive after outplanting. Balisky *et al.* (1995) referred to evidence of root deformation even before root density in walled container systems had increased sufficiently to facilitate normal extraction, handling, and transportation. The findings of Selby and Seaby (1982), concerning the short period after seed germination when seedlings develop primary lateral roots, are relevant to this rapid root deformation; these authors attributed the instability of outplanted pines to the lack of properly oriented primary lateral support roots and the inability of these seedlings to generate new primary lateral roots.



$$\text{Soil-space Ratio} = \frac{\text{soil surface area (Cm}^2\text{)}}{\text{Mean seedling growing space (Cm}^2\text{)}}$$

Conclusion

McGilvray and Barnett (1982) and Barnett and Brissette (1986) questioned whether "balanced seedlings" with low shoot:root ratios were necessary or desirable in container rearing. Seedlings are often held in the nursery for extended periods to lower shoot:root ratios to predetermined specifications, while the crop is subjected to a low nitrogen hardening regime. During hardening, root growth is being elaborated into the confined container soil. Nursery rearing of container stock should delay as much of this very active root growth as possible until the seedling arrives on the outplanting site, to access a maximum of new soil volume for water and nutrient acquisition. The present study has shown that the production of densely rooted soil plugs, on seedlings that are "better balanced" (low shoot: root ratio), can decrease field growth rates. This supports Balisky and Burton (1997), who observed that conventionally reared conifer seedlings, submitted to extended hardwall container residence time, elaborated the majority of new roots into cold soil layers from active growing points at the bottom of the soil plug as opposed to rooting from the sides of the soil plug into comparatively warmer soil layers.

If the production of fragile-rooted soil plugs were adopted into operational growing regimes, then shipment of seedlings to outplanting sites in the nursery growth container cells would minimize soil loss (Carlson 1983) and extraction of the seedling would occur at the moment of planting. Alternatively, rearing systems incorporating air pruned mesh-covered plugs which do not require excessive root growth to produce soil plug stability, should be considered (Orlander 1982; Balisky *et al.* 1995).

The advantages to field growth rates for seedlings with juvenile, responsive rooting systems suggest that conventional stock specifications that demand firm, well-rooted soil plugs that are easily extracted, handled, and transported without soil loss, need reassessment. Increased growth rates during the critical early outplant period, as root density in nursery-produced soil plugs is decreased, lead us to recommend the production of light-rooted plugs in both walled container systems and in mesh-covered, free-standing soil plugs. This can be accomplished by reducing residence time in containers and modifying cultural practices designed to produce low shoot:root ratios that are more appropriate for bare-root stock.

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